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RATES OF PHOTOSYNTHESIS AND PHYTOPLANKTON GROWTH IN SHAGAWA LAKE, MINNESOTA

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Integral photosynthetic rates and growth rates of phytoplankton were measured before, during, and after a bloom of Aphanizomenon, which occurred in August 1970. The size of the population increased during the bloom despite decreasing specific production rates, probably because the dominant algal became more buoyant and decreased its sinking rate. The effects of changing the specific production rates and specific loss rates are demonstrated by comparing the integral photosynthetic rates and chlorophyll concentrations that would prevail under steady state conditions. (EPA)

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RATES OF PHOTOSYNTHESIS AND PHYTOPLANKTON GROWTH IN SHAGAWA LAKE, MINNESOTA

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ABSTRACT

Average concentrations of chlorophyll *a* at 6 localities in Shagawa Lake were between 15 and 25 mg m^{-3} during June and July, 1970, they increased to 150 mg m^{-3} in late August, and decreased rapidly in early September.

Daily maximum specific photosynthesis and stored phosphorus in the plankton both decreased while population densities increased most rapidly. Rapid growth probably stopped because the rate of chlorophyll synthesis exceeded the rate of phosphorus uptake.

The theoretical limits of daily integral photosynthesis imposed by the attenuation coefficients for photosynthetically active radiation are calcualted for the observed ranges of daily maximum specific photosynthesis and chlorophyll concentrations. High attenuation coefficients probably prevented population densities from becoming high enough to utilize all the dissolved phosphorus in the water during the period of most rapid growth.

Specific rates of production and loss of particulate organic carbon in the mixed layer (epilimnion) were both highest just before rapid growth began. Specific rates of loss decreased more rapidly than specific rates of production to produce high specific rates of change during August. Loss rates probably decreased during August because the dominant alga, Aphanizomenon, became more buoyant. The rapid decrease of population densities in early September occurred because loss rates suddenly increased, probably because the populations's buoyancy regulation became less efficient.

A balance equation for the quantity of particulate organic carbon in the mixed layer beneath a unit surface area is used to estimate steady states for integral photosynthesis and chlorophyll concentrations from the optical conditions, rates of maximum specific photosynthesis, and rates of loss that prevailed in the lake.

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SECTION I

CONCLUSIONS

1. Population densities of phytoplankton in Shagawa Lake were relatively constant during early summer, 1970. Population densities of Aphanizomenon increased most rapidly during a bloom that occurred in August, and they decreased rapidly during the first week of September.

2. The phytoplankton were stratified at the surface of the epilimnion during the bloom but not at other times.

3. The photosynthetic capacity of the phytoplankton as measured by the specific photosynthesis at the depth where illumination is optimal increased during the month before the bloom but decreased during the bloom.

4. Population densities increased rapidly during the bloom because specific loss rates decreased more rapidly than specific production rates. The stratification of the phytoplankton during the bloom suggests that specific loss rates decreased because the algae became more buoyant.

5. Phosphorus is a limiting nutrient for the phytoplankton in Shagawa Lake, but phytoplankton production appeared to be limited not by nutrients but by high attenuation coefficients for photosynthetically-active radiation.

6. Steady state population densities under the physical conditions that prevailed are estimated with a balance equation for the quantity of particulate organic carbon in the mixed layer beneath a unit of lake surface.

SECTION II

RECOMMENDATIONS

Although maximum population densities of phytoplankton in Shagawa Lake during 1970 appeared to be limited by high attenuation coefficients for photosynthetically active radiation rather than by nutrient concentrations, phosphorus could be made to limit population densities by reducing the influx from the Ely Municipal Sewage Treatment Plant, which contributed about 70% of the lake's phosphorous.

A monitoring program should be continued after the new treatment plant begins operation in 1972 in order to ascertain the nature of the lake's response. A minimal program should include measurements of the following: integral photosynthesis, chlorophyll concentrations, concentrations of particulate organic material, total and soluble phosphorus, extractable phosphorus in the net plankton, and algal counts. These should be sampled at ten-day or two-week intervals during the open-water season.

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SECTION III

INTRODUCTION

Photosynthesis and nutrient uptake have been studied intensively in order to understand fluctuations of phytoplankton abundance, but studies of these processes cannot indicate whether population densities are increasing, decreasing, or stationary. Population densities depend upon rates of production and loss; the effects of photosynthesis on population densities therefore can be defined only if photosynthesis and population densities are measured in compatible units or if both production and losses are measured. Rates of flux from nutrient pools also depend upon rates of production and loss of phytoplankton (Dugdale 1967). Since loss rates are usually neglected, studies of relationships between nutrients and phytoplankton are usually inconclusive (Fogg and Walsby 1971).

Most pelagic photosynthesis is accomplished by phytoplankton circulating in the epilimnion. Thus the epilimnetic phytoplankton functions as a unit. If photosynthesis is measured in terms of daily carbon assimilation beneath a unit surface, then the quantity of particulate organic carbon associated with the phytoplankton beneath a unit of surface in the epilimnion is an equivalent measure of population density. There is no satisfactory way to determine how much of the particulate organic carbon is associated with phytoplankton, but the phytoplankton is only one constituent of a larger pool of reduced particulate carbon that also contains zooplankton, bacteria, and organic detritus. Organic detritus may comprise 20-80% of the particulate organic material in lake water (Wright 1959), and it, like zooplankton and bacteria, is ultimately produced by photosynthesis. Because each group of organisms participates in the degradation of organic material produced by algal photosynthesis and because many of the chemical changes that occur in lakes depend more upon rates of production and destruction of particulate organic material than upon population dynamics of individual organisms, it is more appropriate from the limnological point of view to assess the dynamics of particulate organic carbon than of phytoplankton or zooplankton alone. Thus our inability to distinguish the quantities of particulate organic carbon associated with each category of living and dead organisms is not a serious disadvantage, because the total quantity of particulate organic carbon in the epilimnion is also a functional ecological unit.

Particulate organic carbon is lost from the epilimnion by

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three separate and unrelated mechanisms -- respiration, excretion, and sinking. It is difficult to measure the rates of these processes individually, but the aggregate loss of particulate organic carbon may be calculated from the rate that it is produced and the rate that its concentration changes.

A balance equation for particulate organic carbon in the epilimnion is formulated in this report, and data from Shagawa Lake are used to calculate specific rates of production, specific rates of change, and specific rates of loss. It is often assumed that phytoplankton blooms occur because production rates increase, but specific rates of production decreased during a bloom that occurred in Shagawa Lake. Population densities increased because the decreased production rates were offset by decreased loss rates. The balance equation is also used to calculate steady state population densities for phytoplankton.

Mathematical models of plankton dynamics tend to be one or the other of two types: time-related models concerned with growth dynamics or depth-related models concerned with productivity in water columns (Patten 1968). However, depth-related models are instantaneous components of time-related models, and an important requirement of a time-related model must therefore be that it incorporate a depth-related model. Also, if a time-related model is to be realistic, it must be formulated in such a way that data can be obtained to test and use it. Talling (1957b) and Vollenweider (1965, 1970) have developed a realistic depth-related model for the daily production of particulate organic carbon by phytoplankton. This may be used as a basis for a realistic time-related model for the dynamics of particulate organic carbon in the mixed layer because the existing quantity of particulate organic carbon may be estimated easily. Thus all the data for evaluating the parameters of a time-related model for particulate organic carbon may be obtained with chemical methods.

SECTION IV

THE LAKE

Phytoplankton are usually much more abundant in Shagawa Lake (Lat. 47° 55' N, Long. 91° 25' W) than in most other lakes in northeast Minnesota. About 80% of the water entering Shagawa Lake comes from the Burntside River which drains Burntside Lake, a large unproductive lake located several km to the west. However, about 70% of the phosphorus and 25% of the total nitrogen entering Shagawa Lake via surface waters come from a municipal sewage treatment plant at Ely on the south side of the lake (Powers et. al. 1972; Fig. 1).

The area of the lake is 9.6×10^6 m^2, its volume is 59.5×10^6 m^3, its maximum depth is 14.7 m, and its mean depth is 6.2 m (Table 1). Many small, rocky islands are scattered throughout the basin.

The salinity of Shagawa Lake is 1.6 meq $liter^{-1}$, which is similar to the salinity of other lakes in northeast Minnesota (Table 2; Bright 1968), but higher than the mean salinity (0.4 meq $liter^{-1}$) of 40 lakes in the Experimental Lakes Area in nearby northwest Ontario (Armstrong and Schindler 1971). The dominant dissolved cations are calcium and magnesium, and the dominant anions are bicarbonate and sulfate.

The effects of the abundant plankton on water chemistry are indicated by the differences between the oxygen concentrations and pH in the epilimnion and those in deeper waters (Table 3). Oxygen is usually present in the deep waters of lakes in northeast Minnesota, but not in the deep waters of Shagawa Lake. It is also notable that the pH may exceed 10 in surface waters but it is near neutrality below 6 m. The pH of surface waters in most lakes of the region is typically neutral or slightly acid (Bright 1968).

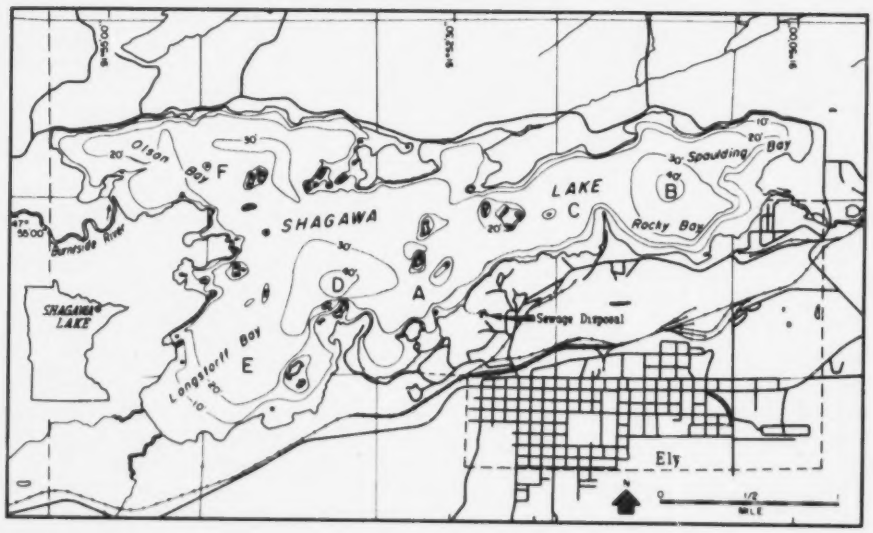

Figure 1. Hydrographic map of Shagawa Lake. Six sampling stations are indicated by the letters A, B, C, D, E, and F.

Table 1. Hydrographic features of Shagawa Lake.

Depth Interval (ft)	Area (10^6 m^2)	(%)	Volume (10^6 m^3)	(%)
0-10	9.64		26.30	44
10-15	7.64	79	10.88	18
15-20	6.66	69	9.49	15
20-30	5.76	60	9.54	16
30-40	1.10	11	3.22	5
40-48	1.01	10	.05	
			59.5	

Surface Area	$9.64 \times 10^6 m^2$
Volume	$59.5 \times 10^6 m^3$
Mean Depth	6.2 m
Maximum Depth	14.7 m

Table 2. Major dissolved ions (mg liter^{-1}) in Shagawa Lake, 19 northeastern Minnesota lakes (Bright 1968) and for a group of 40 lakes in Ontario just north of Minnesota (Armstrong and Schindler 1971).

	Shagawa Lake	Mean for 19 northeastern Minnesota lakes	Mean for 40 Ontario lakes
Calcium	9.90	10.2	1.6
Magnesium	3.36	3.0	0.9
Sodium	2.0	1.5	0.9
Potassium	0.6	0.8	0.4
Bicarbonate	26.8	39.0	3.8
Chloride	0.1	0.1	1.4
Sulfate	13.8	5.7	3
Salinity (meq/l)	1.62	1.7	0.4

Table 3. Temperature, oxygen, and pH at depth intervals at Station D.

Depth (m)	29 July 1967			14 August 1967			1 August 1970	3 August 1970	
	Temp (°C)	O_2 (mg/l)	pH	Temp (°C)	O_2 (mg/l)	pH	Temp (°C)	Temp (°C)	O_2 (mg/l)
0	21.2			21.3	10.6	9.7			
1	21.2	10.5	10.2	21.3		9.7	23.0	21.8	7.0
2	21.0	10.2	10.0	21.3	10.3	9.7	23.0	21.8	7.2
3	20.8	9.5	9.8	21.0			22.8	21.8	7.2
4	20.2	9.2	9.6	19.7	6.0	8.2	22.7		
5	19.8			19.4			21.9	21.7	7.0
6	19.6	5.7	7.7	19.3	5.8	8.1	21.2	20.8	7.0
7	18.8			19.2			20.8		
8	18.2	2.6	7.1	18.9	5.1	7.8	20.4	20.8	6.5
9	17.4			18.9			19.8	20.8	6.5
10	17.3	0.6	7.0	18.8	4.0	7.5	19.2		
11	17.3			18.8			18.8	18.8	1.0
12	17.2	0.2	7.0	18.1	0.0	7.2	15.7	15.6	0.2
13	16.6			16.8					

SECTION V

METHODS

Population densities of the phytoplankton, rates of photosynthesis, and phosphorus concentrations were measured during the spring and summer of 1970 in water samples from 6 localities (Fig. 1).

Gross photosynthesis by the phytoplankton was measured with the oxygen light-dark bottle method (Strickland and Parsons 1968, Talling 1957a). The daily total gross photosynthesis (integral photosynthesis) beneath a unit surface was measured in situ at Station A. Water samples were collected at depth intervals, and portions of each sample were transferred immediately to transparent and opaque B.O.D. bottles (300 ml capacity). The bottles were placed in holders, and the holders were suspended at the depths from which the samples were collected (usually 0, 0.2, 0.5, 1, 1.5, 2, and 3 m). The bottles were suspended for 6-hr incubation periods, from 1200 to 1800 hrs. Thus almost 50% of the daily gross photosynthesis was measured.

Water samples were also collected at the surface from each of the other 5 localities immediately before each experiment. These samples were also transferred to pairs of light and dark bottles, placed in holders, and the holders were attached to a bar between two buoys so that the bottles were suspended at a depth of 0.5 m, where the average light intensity was optimal for photosynthesis. This depth was ascertained from previous depth profiles of photosynthesis obtained from samples incubated in situ at depth intervals.

Oxygen concentrations in the transparent and opaque bottles were determined immediately after each experiment; 203 ml samples from the B.O.D. bottles were titrated with 0.025 N $Na_2S_2O_3$ delivered from 10-ml automatic burets, with which oxygen concentrations may be estimated to the nearest 0.02 mg oxygen liter^{-1}. Daily gross carbon assimilation was computed from the oxygen changes with the equation,

$$p = F \frac{2\ (LB - DB)}{P.Q.}$$

$$= .625\ (LB - DB)$$

where p is gross photosynthesis (mg carbon liter^{-1} dy^{-1}); LB and DB are the oxygen concentrations (mg liter^{-1}) in the transparent and opaque bottles; PQ is the photosynthetic quotient (moles oxygen produced/moles carbon assimilated),

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which was assumed to have a value of 1.2 (Westlake 1963, Strickland 1965); and F is the ratio of the molecular weights of carbon and oxygen (0.375). It should be emphasized that the estimates of daily gross photosynthesis are somewhat low because the days were longer than twice the 6-hr incubation interval.

Daily integral photosynthesis (Σp; mg carbon m^{-2} dy^{-1}) at Station A was estimated by determining the area enclosed by the depth profiles with a planimeter. The photosynthesis that occurred in the bottles incubated at the average depth of optimal illumination was a measure of daily maximum photosynthesis at the localities from which the samples were collected. Maximum specific photosynthesis (p_{max}; mg carbon [mg chlorophyll]$^{-1}$ dy^{-1}) was estimated as the ratio of maximum photosynthesis to chlorophyll concentrations (p_{max}:c) in the samples incubated at optimal illumination.

Concentrations of chlorophyll *a* in the water samples used for the photosynthesis experiments were determined by the SCOR/UNESCO procedure (Strickland and Parsons 1968). Between 250 and 500 ml of sample were filtered through Millipore type HA membrane filters. The filters were macerated in a tissue grinder that contained 90% acetone, and the absorbancie of the acetone extracts were determined after 1/2 hr.

Concentrations of total and soluble phosphorus were determined with the ammonium molybdate method, using stannous chloride as the reductant (Amer. Public Health Association 1965). Concentrations of total phosphorus were determined in unfiltered samples after they were digested with $K_2S_2O_8$ in a pressure cooker (Menzel and Corwin 1965). Concentrations of soluble phosphorus were determined on samples that were not filtered or digested. The concentrations of soluble phosphorus are probably overestimated somewhat because the reagents may have hydrolyzed some of the particulate phosphorus. The extractable phosphorus content of the net plankton was determined by the procedure described by Fitzgerald and Nelson (1966).

PHYTOPLANKTON, CHLOROPHYLL, AND PHOTOSYNTHESIS

The planktonic algae in Shagawa Lake were not examined intensively during the summer of 1970, when the lake was studied most intensively, but periodic examinations indicated that Anabaena was dominant in June. Aphanizomenon appeared in late June, it became conspicuous during July, and very abundant in August, when it represented virtually the entire algal biomass. A rapid decrease occurred in early September.

Mean chlorophyll concentrations in surface waters fluctuated between 11 and 21 mg m^{-3} during June and July, increased to 146 mg m^{-3} on August 31, and decreased again during September and October (Fig. 2, Table 4).

Chlorophyll concentrations at the 6 stations were more similar to each other on the sampling days in June, July, and early August than in late August, when the coefficient of variability increased to 69% (Table 5). Although the variance increased during August, concentrations were not consistently higher at any one locality than at others.

Chlorophyll was probably concentrated by local water movements at three localities on 6 August, 31 August, and 5 September, so the data from these localities were excluded from the computations of the means and variances for those dates (Table 4). The most extreme example was on 31 August, when the concentration at the surface was 977 mg m^{-3} at Station A but between 67 and 321 mg m^{-3} at the other localities.

The variation that may occur at a locality during a single day is exhibited by the chlorophyll concentrations at Station D on 1 August, 1968 (Table 6). Chlorophyll concentrations above 4 m at 1200 hr (34-38 mg m^{-3}) were 50% higher than at 0600 hr (24-26 mg m^{-3}). Furthermore, the highest specific photosynthesis (P) was measured at the surface for the samples incubated *in situ* during the morning, but at 0.5 m for the samples incubated in the afternoon. As a result of these variations, daily integral photosynthesis on 1 August, 1968, would be 1.9 g carbon m^{-2} dy^{-1} if calculated from the morning experiment and 2.5 g carbon m^{-2} dy^{-1} if calculated from the afternoon experiment. The skies were cloudless the entire day; photosynthesis is apparently less vulnerable to inhibition by high light intensities in the morning than afternoon. Thus, the low rates of photosynthesis at the surface that are evident in the depth profiles for 1970 (Fig. 3) are perhaps largely photoperiodic responses that are characteristic features of incubations performed after noon (1200-1800 hrs).

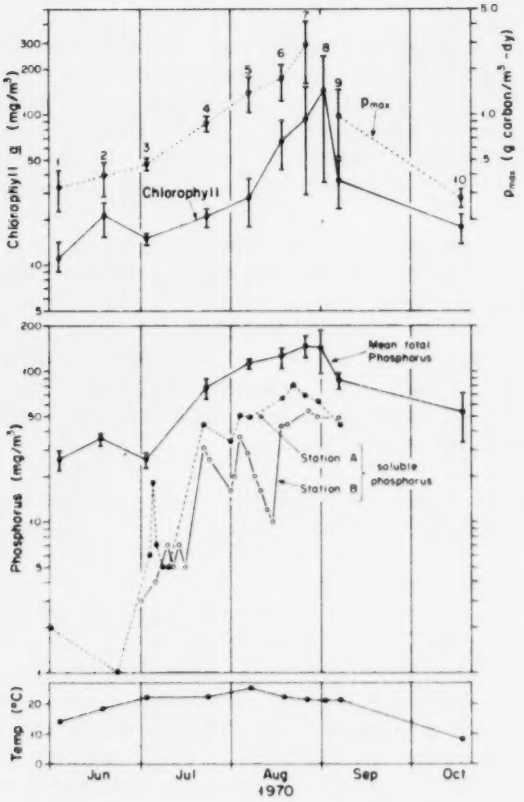

Figure 2. Mean concentrations of chlorophyll a, total phosphorus, and mean maximum photosynthesis (p_{max}) in surface waters of Shagawa Lake at Stations A-F during 1970. The standard deviation for each date is indicated by the length of the line through each datum point. Concentrations of soluble phosphorus at Stations A and B and temperatures of surface water at Station A are also indicated.

Table 4. Chlorophyll concentrations (c, mg m^{-3}), maximum photosynthesis (p_{max}, g carbon m^{-3} dy^{-1}), maximum specific photosynthesis (P_{max}, mg carbon (mg chlorophyll)$^{-1}$ dy^{-1}), integral photosynthesis (Σp, g carbon m^{-2} dy^{-1}), the depth z_i (meters), concentrations of total phosphorus (F_t, mg m^{-3}) and temperatures in surface waters (T, °C) of Shagawa Lake in 1970. Numbers in parentheses were excluded from computations of the means ($\bar{x}$) and standard deviations (S.D.).

Experiment # and Date	Station	c	p_{max}	P_{max}	Σp	z_i	F_t	T
1, 3 June	A	8	0.29	41	0.88	3.0	23	14
	B	9	0.23	25			27	
	C	10	0.28	29			26	
	D	11	0.34	31			22	
	E	21	0.53	25			32	
	F	9	0.28	31			25	
	$\bar{X}$	11	0.33	30			26	
	S.D.	5	.11	6			4	
2, 17 June	A	16	0.31	20	0.45	1.4	35	18
	B	20	0.40	20			39	
	C	20	0.36	18			38	
	D	15	0.28	18			31	
	E	25	0.42	17			35	
	F	30	0.58	19			36	
	$\bar{X}$	21	0.39	19			36	
	S.D.	6	.11	1			3	

Experiment # and Date	Station	c	p_{max}	P_{max}	Σp	z_i	F_t	T
3, 2 July	A	17	0.46	27	0.94	2.0	32	22
	B	14	0.47	34			27	
	C	16	0.52	33			26	
	D	13	0.37	28			25	
	E	15	0.49	33			24	
	F	16	0.51	33			24	
	$\bar{X}$	15	0.47	31			26	
	S.D.	1	0.05	3			3	
4, 22 July	A	18	0.88	50	1.04	1.2	97	22
	B	27	1.08	39			86	
	C	22	0.84	38			70	
	D	19	0.87	46			73	
	E	20	0.85	43			79	
	F	21	0.75	36			58	
	$\bar{X}$	21	0.88	42			77	
	S.D.	3	.11	5			14	
5, 6 August	A	25	1.23	52	1.35	1.1	116	25
	B	(120)	(2.26)	(19)			(180)	
	C	44	1.96	45			118	
	D	27	1.48	54			109	
	E	28	1.35	47			110	
	F	16	0.99	60			104	
	$\bar{X}$	28	1.40	52			111	
	S.D.	10	0.36	6			6	
6, 17 August	A	108	2.45	32	2.14	0.9	157	22
	B	54	1.52	28			110	
	C	75	2.17	29			110	
	D	42	1.32	31			123	
	E	50	1.36	27			108	
	F	72	1.46	19			142	
	$\bar{X}$	67	1.71	28			125	
	S.D.	24	.48	5			20	

Experiment # and Date	Station	c	p_{max}	P_{max}	Σp	z_i	F_t	T
7, 25 August	A	40	1.72	43	2.13	1.2	123	21
	B	198	4.75	24			193	
	C	87	2.80	32			129	
	D	71	2.73	39			133	
	E	121	4.06	34			158	
	F	27	1.16	43			161	
	$\bar{X}$	91	2.87	36			150	
	S.D.	62	1.36	7			26	
8, 31 August	A	(977)			2.70		(433)	21
	B	102					123	
	C	117					142	
	D	321					223	
	E	124					131	
	F	67					102	
	$\bar{X}$	146					144	
	S.D.	100					46	
9, 5 Sept	A	29	0.87	30	1.41	1.6	85	21
	B	29	0.47	10			98	
	C	37	0.92	25			87	
	D	60	1.83	31			94	
	E	(185)	(3.41)	(18)			(153)	
	F	31	0.87	28			70	
	$\bar{X}$	37	0.99	25			87	
	S.D.	13	0.50	9			11	
10, 17 October	A	16	0.25	16	0.52	2.1	92	
	B	18	0.23	12			56	
	C	16	0.26	17			51	
	D	14	0.28	19			44	
	E	18	0.32	18			42	
	F	26	0.33	13			41	
	$\bar{X}$	18	0.28	16			54	
	S.D.	4	0.04	3			19	

Table 5. Coefficients of variabllity (S.D./$\bar{X}$) for chlorophyll concentrations at 6 localities in Shagawa Lake.

Date	Experiment	Mean ($\bar{X}$)	Standard deviation (S.D.)	$\frac{S.D.}{\bar{X}}$ (%)
3 June	1	11	4.7	43
17 June	2	21	5.7	27
2 July	3	15	1.5	10
22 July	4	21	3.2	15
6 August	5	28	10.1	36
17 August	6	67	23.9	36
25 August	7	91	62.4	69
31 August	8	146	100.2	69
5 September	9	37	13.2	36
17 October	10	18	4.2	23

Table 6. Concentrations of chlorophyll a at 0600 hrs and 1200 hrs and rates of photosynthesis measured in the morning (0600-1200 hrs) and in the afternoon (1200-1800 hrs) at Station D on 1 August 1968.

	Depth	Chlorophyll a	Photosynthesis	
	(m)	mg m^{-3}	p g carbon m^{-3} dy^{-1}	P mg carbon (mg chl)$^{-1}$ dy^{-1}
0600 hrs	0.0	26	1.63	63
	0.5	24	1.18	49
	1.0	24	0.78	33
	2.0	24	0.18	18
	4.0	25	0.02	1
1200 hrs	0.0	36	1.29	36
	0.5	38	1.60	43
	1.0	35	1.25	36
	2.0	36	0.32	9
	4.0	34	0.07	2

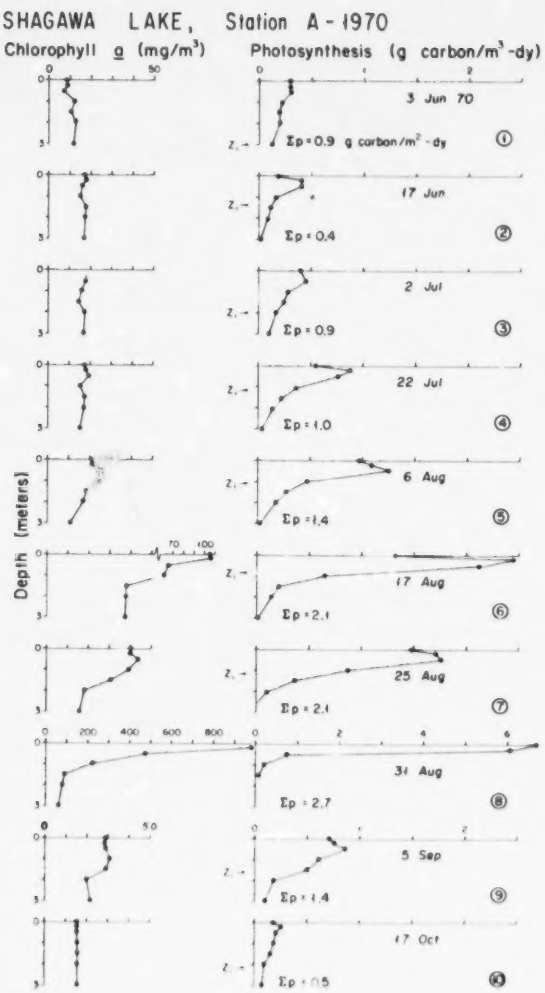

Figure 3. Concentrations of chlorophyll a in the upper 3-meters and depth profiles of photosynthesis during 10 experiments at Station A during 1970. Integral photosynthesis (Σ p) is indicated for each experiment.

Chlorophyll concentrations during August were typically higher at the surface than at 2 or 3 m (Fig. 3). This stratification was probably related in part to a weak thermal gradient between 2 and 3 m that may develop on calm, sunny days (Table 3) and in part to the buoyancy of the Aphanizomenon colonies.

Maximum photosynthesis (p_{max}) at each station was measured by incubating surface samples from each locality simultaneously at Station A at the depth where the average daily illumination was optimal for photosynthesis, which was usually 0.5 m. Maximum photosynthesis, which is a simple product of the chlorophyll concentration in a sample (c) and maximum specific photosynthesis (P_{max}), varied approximately 10-fold in correspondence with the 10-fold variations of chlorophyll, from 0.33 g carbon m^{-3} dy^{-1} for experiment 1 to 3.22 g carbon m^{-3} dy^{-1} for experiment 7 (Table 4, Fig. 2). (Maximum photosynthesis could not be evaluated for experiment 8 because chlorophyll concentrations at Station A where the samples were incubated were so high that light intensities were suboptimal at all depths.)

Mean maximum specific photosynthesis (P_{max}) decreased from 30 to 19 mg carbon (mg chlorophyll)$^{-1}$ dy^{-1} during June (experiments 1 and 2), increased to 52 mg carbon (mg chlorophyll)$^{-1}$ dy^{-1} in early August (experiment 5), and decreased again during August and September (Fig. 4-A).

Maximum specific photosynthesis varied with temperatures in lakes studied by Talling (1957a, 1966) and in Lake Minnetonka (Megard 1972) and with population densities of the phytoplankton in other lakes (Wright 1960, Findenegg 1965). However, there was no consistent relationship between maximum specific photosynthesis and either temperatures or population densities in Shagawa Lake. There was apparently an inverse relationship between maximum specific photosynthesis and chlorophyll concentrations during experiments 1, 5, and 7, but not during the others (Fig. 5). Maximum specific photosynthesis decreased but the temperatures increased in June (Figs. 2 and 4-A). Maximum specific photosynthesis decreased during August, when population densities fluctuated and temperatures were virtually constant. The most consistent relationship was between maximum specific photosynthesis and the extractable phosphorus content of the phytoplankton (Figs. 4-A and 4-C).

The decrease of maximum specific photosynthesis during the time when chlorophyll concentrations increased most rapidly demonstrates that growth (i.e. chlorophyll synthesis

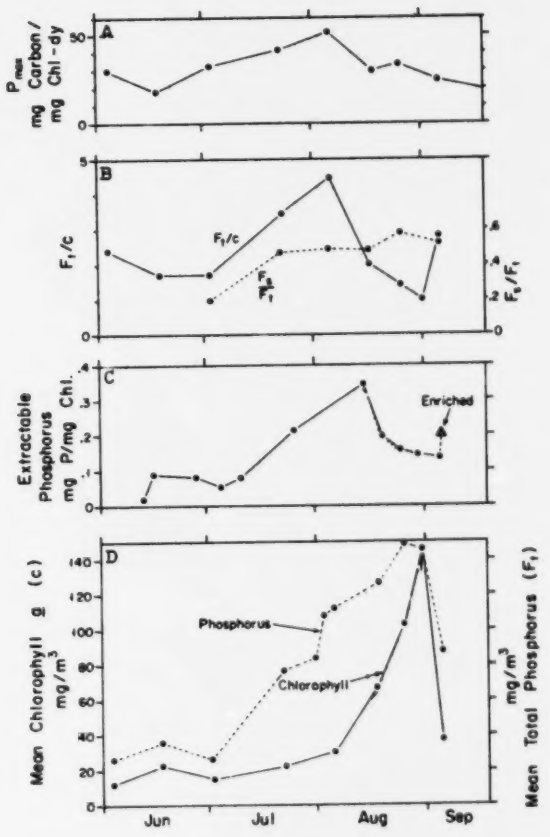

Figure 4. A) Maximum specific photosynthesis, B) the ratio of total phosphorus to chlorophyll a (F_t/c) and the ratio of soluble to total phosphorus (F_s/F_t), C) the extractable phosphorus in net plankton, and D) concentrations of total phosphorus and chlorophyll a in surface waters.

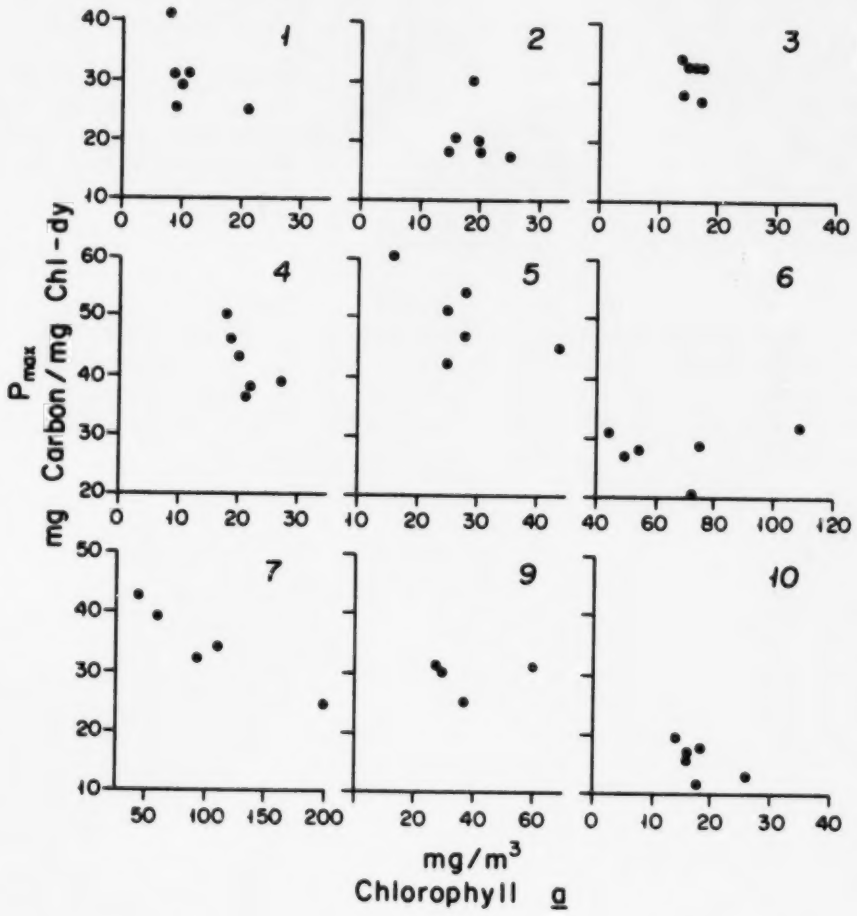

Figure 5. The relationship between maximum specific photosynthesis (P_{max}) and chlorophyll for all experiments except experiment 8, when P_{max} could not be evaluated.

in this case) and photosynthesis are separate processes. A similar "uncoupling" of photosynthesis and growth occurs at Windermere, where specific photosynthesis remains high after cell division is limited by low silica concentrations (Talling 1966).

Integral photosynthesis (Σp) was measured at Station A by incubating samples at depth intervals in situ (Fig. 3, Table 4). Variations of integral photosynthesis generally corresponded to variations of population densities, with exceptions due to variations of maximum specific photosynthesis. Integral photosynthesis at this station varied from 0.45 g carbon m^{-2} dy^{-1} for experiment 2 (17 June) to 2.70 g carbon m^{-2} dy^{-1} for experiment 8 (31 August). If a photosynthetic zone is defined to be the depth above which photosynthesis occurs, then the depth profiles of photosynthesis indicate that the photosynthetic zone was somewhat more than 3-m thick at other times. It was only 1.5 m thick at Station A on 31 August (experiment 8) when chlorophyll concentrations at the surface reached 977 mg m^{-3}.

The weighted mean value of integral photosynthesis at Station A from early June through late October was 1.2 g carbon m^{-2} dy^{-1}. The total gross photosynthesis at this station for the 5-month period is therefore 180 g carbon m^{-2}.

SECTION VII

PHOSPHORUS

Mean concentrations of total phosphorus in surface waters were between 25 and 40 mg m^{-3} during June (Fig. 2, Table 4). They increased to a maximum of 150 mg m^{-3} in late August, and declined to 55 mg m^{-3} in October.

Concentrations of soluble phosphorus were less than 2 mg m^{-3} in June. There was a sharp increase in early July, and the highest concentrations were 50-80 mg m^{-3} in August (Fig. 2).

Many tourists visit Ely during the summer and the increased phosphorus concentrations in the lake after 4 July may be due in part to an increased phosphorus influx from sewage effluents, but preliminary calculations indicate that the quantity contributed by sewage cannot account for all of the increase in the lake. The sudden decrease in August occurs when the number of tourists decrease, but the low ratio of total phosphorus to chlorophyll (F_t/c, Fig. 4B) indicates that much of the phosphorus was incorporated in the phytoplankton at that time. Therefore much of the phosphorus may have been transported out of the water at the end of the bloom by algae sinking to the lake sediments.

Mean concentrations of total phosphorus in surface waters increased from 26 mg m^{-3} to 150 mg m^{-3} during the 54-dy period between 2 July and 25 August, a net increase of 124 mg m^{-3}. The increase was approximately linear (Fig. 4-D), and the average rate of increase was 2.3 mg m^{-3} dy^{-1}. Concentrations at Station A were about the same at all depths above 6 m at any time during this period (Table 7). If the mean subsurface concentration in the upper 6 m at all stations increased as much as the mean surface concentrations, then the total quantity of phosphorus in the water above 6 m ($46.7 \times 10^6 m^3$) increased from 1.3×10^9 mg to 7.0×10^9 mg, or 110 kg dy^{-1}.

The effect of severe wind-induced turbulence on the quantity of phosphorus in Shagawa Lake is illustrated by 2 series of analyses on 1 and 3 August (Table 8), before and after a severe storm on 2 August. The mean concentration of total phosphorus in the water above 6 m was 19 mg m^{-3} higher after the storm than before it, a 21% increase. The total quantity of phosphorus in the water above 6 m increased 0.9×10^9 mg (900 kg). It should be noted, however, that the rate that phosphorus increased was accelerated only temporarily as a result of the storm.

Table 7. Concentrations of total phosphorus (mg m^{-3}) at Station A in 1970.

depth (m)	June		July		August				October
	3	17	2	22	6	17	25	31	17
0.2	22.6	35.4	33.0	96.9	92	157	123	433	92
0.5	22.2	33.4	32.4	92.9	99	139	122	266	89
1.0	24.7	35.8	33.3	95.6	117	143	124	209	93
1.5	26.9	37.2	33.3	90.6	124	121	116	138	94
2.0	29.0	34.8	34.7	86.8	147	136	110	131	76
3.0	29.0	32.0	36.0	81.1	166	131	104	119	63
5.0				117	101	124	108	107	74
6.0	58.6	60.1	36.0						

Table 8. Phosphorus concentrations (mg m^{-3}) at stations A-F and the quantity of phosphorus above 6-m depth before and after a storm on 2 August, 1970.

1 August

Depth (m)	A	B	C	D	E	F	$\bar{X}$	Quantity of phosphorus above 6 m
				Total Phosphorus				
0.5	93	89	85	64	87	64	81	
3.0		68	66	80	104	80	79	
5.0	69				127		97	4.0×10^9 mg
6.0		67	80	107		107	108	
10.0		409						
11.0				218				
				Soluble Phosphorus				
0.5	36	20	23	35	59	33	34	
3.0		19	24	36	68	52	40	
5.0	35				92		63	
6.0		32	45	177		73	82	
10.0		409						
11.0				228				

3 August

				Total Phosphorus				
0.5	102	94	115	109	113	106	107	
3.0	107	92	119	111	117	109	109	4.9×10^9 mg
5.0	107		82		114	103	101	
6.0		95		111			102	
10.0		456						
11.0				234				
				Soluble Phosphorus				
0.5	52	37	36	71	78	68	57	
3.0	57	31	34	73	83	68	58	
5.0	55		42		90	67	63	
6.0		27		73			50	
10.0		482						
11.0				246				

The increase of phosphorus during July and August raises the question as to whether there was a net deposition or a net release of phosphorus from the sediments. The issue may be resolved in this case by solving the equation,

$$\frac{dF}{dt} = I + S - L, \qquad (2)$$

where I is the rate of influx from the watershed, primarily from the sewage treatment plant, S is the rate of exchange with the sediments (the sign of S will be positive if phosphorus was released, and negative if phosphorus was deposited), and L is the loss to the outlet. The rate of change (dF/dt) was evaluated above (110 kg dy^{-1}). The equation may be solved for S because the influx from the sewage treatment plant (I) and the loss at the outlet (L) may be evaluated with data obtained by the staff of the Shagawa Lake Eutrophication Project at Ely, but these data are not yet available.

The relationships between concentrations of total phosphorus and chlorophyll are shown in Fig. 6. There was no apparent correlation between phosphorus and chlorophyll during June, July, and October (experiments 1, 2, 3, 4, and 10), but there were linear relationships in August and September, during and immediately after the period when chlorophyll concentrations increased most rapidly (experiments 5, 6, 7, 8, and 9). The slope of the regression equation for experiments 5, 6, and 7 (1.33 $\pm$ 0.61 mg chlorophyll [mg phosphorus]$^{-1}$) is less than but not significantly different from the slope of the equation for experiments 8 and 9 (2.01 $\pm$ 0.32 mg chlorophyll [mg phosphorus]$^{-1}$).

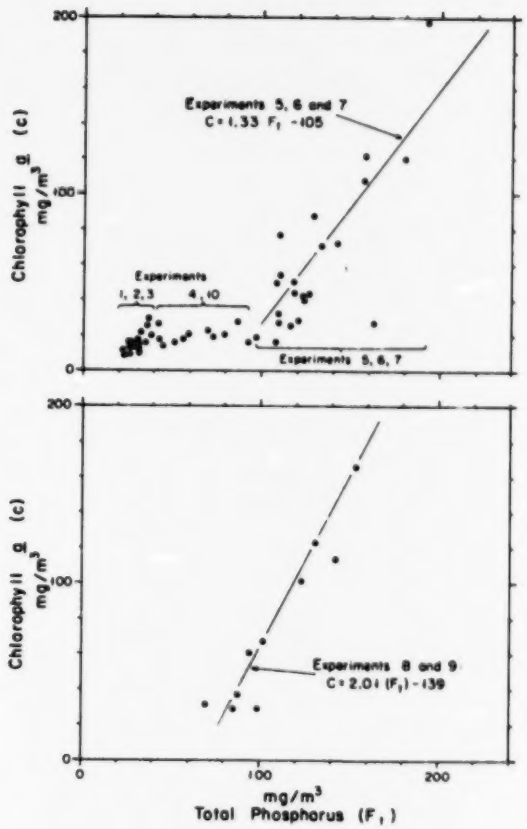

Figure 6. The relationships between concentrations of chlorophyll a and total phosphorus in surface waters of Shagawa Lake.

SECTION VIII

EXTRACTABLE PHOSPHORUS AND PHYTOPLANKTON GROWTH

Phosphorus that is extractable from algae by boiling water represents surplus phosphorus stored by the algae as a result of luxury consumption (Fitzgerald and Nelson 1966). The fluctuations of extractable phosphorus described here pertain to phosphorus in material retained by a #25-mesh plankton net. This material includes zooplankton and detritus as well as algae, but the data are presumed to reflect changes in the extractable phosphorus of the phytoplankton, particularly during August, when virtually all the algae were large enough to be retained by a net and zooplankton were not abundant.

The extractable phosphorus in the net plankton was less than 0.1 mg (mg chlorophyll)$^{-1}$ during June and early July (Fig. 4-C, Table 9). Thereafter, extractable phosphorus increased to a maximum of 0.34 mg (mg chlorophyll)$^{-1}$ in mid-August, indicating that the algae were storing phosphorus. Extractable phosphorus then decreased during the time that chlorophyll concentrations increased most rapidly, and it fell to 0.13 mg (mg chlorophyll)$^{-1}$ in early September.

The extractable phosphorus content expressed in terms of the dry weight of the net plankton (Table 9) is approximately the same as that of algae grown in culture media, even though concentrations of soluble phosphorus in the lake (1-50 µg liter^{-1}) are much lower than the concentrations that limit growth in cultures (1.6 mg liter^{-1}). The extractable phosphorus of net plankton in Shagawa Lake increased from 0.17 mg (100 mg dry weight)$^{-1}$ in early July to a maximum of 1.2 mg (100 mg dry weight)$^{-1}$ in August. In contrast the extractable phosphorus content of blue-green algae is about 0.05 mg (100 mg dry wt)$^{-1}$ in cultures that are phosphorus deficient (less than 1.6 mg liter^{-1}) and about 0.4 mg (100 mg dry wt)$^{-1}$ in cultures that contain surplus phosphorus (7.2 mg liter^{-1}) (Fitzgerald and Nelson 1966).

Mean chlorophyll concentrations began to increase rapidly 34 days after phosphorus concentrations began to increase. During the 34-day period before the rapid increase of chlorophyll, the ratio of total phosphorus to chlorophyll (F_t/c) in the water increased from 1.7 to 4.4. Maximum specific photosynthesis (P_{max}) also increased, perhaps because the extractable phosphorus content of net plankton increased (Fig. 4).

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Table 9. Extractable phosphorus in the net plankton from Shagawa Lake during 1970.

Date	mg phosphorus / mg chlorophyll	mg phosphorus / 100 mg dry wt
12 June	0.02	0.06
15 June	0.09	0.32
27 June	0.08	0.28
4 July	0.05	0.17
10 July	0.08	0.29
25 July	0.21	0.74
14 August	0.34	1.2
19 August	0.19	0.66
24 August	0.15	0.52
29 August	0.14	0.49
4 Sept	0.13	0.46

During the 25 days that chlorophyll increased most rapidly (6 Aug-31 Aug) there were decreases in the ratio of phosphorus to chlorophyll in the water (F_t/c), in maximum specific photosynthesis (P_{max}), and in extractable phosphorus in the net plankton. However, total phosphorus and the fraction of the total phosphorus in the water that was soluble (F_s/F_t) increased slightly. Thus the phosphorus content of the algae decreased while they grew most rapidly even though concentrations of dissolved phosphorus in the water remained high.

An experiment was performed during the period that population densities were decreasing that provides direct evidence that the phytoplankton retained the ability to take up phosphorus. A water sample was enriched with 2 mg liter^{-1} phosphorus on 3 September and incubated 24-hr at the depth where illumination was optimal. The extractable phosphorus increased from 0.13 mg (mg chlorophyll)$^{-1}$ before to 0.20 mg (mg chlorophyll)$^{-1}$ after enrichment and incubation (Fig. 4-C).

The data suggest that the duration of rapid growth, and hence the chlorophyll concentrations at the time when rapid growth stops may have depended upon the time required for the extractable phosphorus content of the phytoplankton to decrease from a maximal to a minimal value. The phytoplankton became phosphorus-deficient because the rate of uptake was less than the rate of loss. The rate of uptake may have been low because the phosphorus in the water may have been in a form that was unavailable, but uptake also may have been suppressed because subsurface light intensities decreased as population densities increased (Kuhl 1962, 1968). Low subsurface light intensities associated with high population densities would tend to suppress phosphorus uptake, but chlorophyll synthesis would be enhanced because of shade adaptation. Talling (1966) observed that the chlorophyll content of algae below the photosynthetic zone in Windermere is about 50% higher than of algae at the surface during the period when population densities of Asterionella increase.

This type of shade adaptation is also exhibited by phytoplankton in Shagawa Lake. The chlorophyll content of phytoplankton in water deeper than 1.5 m was higher than that of phytoplankton in shallower water during July and August 1967 (Table 10). The chlorophyll content was 3 mg (10^9 algae)$^{-1}$ in all samples from the surface on 14 August, despite the wide range of population densities, but it was 12 and 15 mg (10^9 algae)$^{-1}$ at depths of 6 and 10 m. The photosynthetic zone was 3-m thick

Table 10. Algal population densities and chlorophyll concentrations in Shagawa Lake on 29 July and 14 August, 1967.

Date	Depth (m)	Temp (°C)	mg chl. 10^{-3}	10^9 algal filaments per m^3	mg Chl. per 10^9 algal filaments
29 July					
Station D	0.5	21.2	104	21.9	5
	1.5		110	21.2	5
	3.0	20.8	69	10.1	7
	6.0	19.6	4	.2	16
	10.0	17.3	3		
	12.0	17.2	1	.1	20
14 August					
Station A	0		24	9.8	3
B	0		138	46.9	3
E	0		30	9.5	3
F	0		56	16.7	3
D	0	21.3	26	8.4	3
	2.0	21.3	30	6.7	4
	4.0	19.7	5	1.6	3
	6.0	19.3	5	.4	12
	10.0	18.8	5	.2	15

on this date and less than 3 m during August, 1970 (Fig. 3). Hence, more than 50% of the algae in the epilimnion experience light intensities which are insufficient for photosynthesis but which apparently stimulate chlorophyll synthesis. The contrasting response of chlorophyll synthesis and phosphorus uptake to low light intensities apparently induces unbalanced growth, and blooms may be self-limiting because phosphorus uptake cannot keep pace with chlorophyll synthesis.

The cellular level of extractable phosphorus is a dynamic equilibrium involving the following rates: uptake of mineral phosphorus, losses of the same through excretion, and transformation to other types of cellular phosphorus via biosynthetic processes. A substantial phosphorus demand would exist to sustain a bloom of the magnitude observed. Considering that phosphorus uptake and storage requires an energy expenditure, it would be reasonable to expect that algae would preferentially utilize orthophosphate available from intracellular pools (here assessed as extractable phosphorus). The rapid decline of extractable phosphorus during the phase of most rapid growth most probably reflected a rapid transformation of stored mineral phosphorus to cellular organic matter.

SECTION IX

NUTRIENT LIMITATION

Powers et al. (1972) added phosphorus, nitrogen, and carbon singly and together to phytoplankton enclosed in 300-liter bags that were suspended in Shagawa Lake during July 14-30 and August 5-24, 1970. Enrichment with phosphorus alone, nitrogen alone, and nitrogen and phosphorus together stimulated chlorophyll production during both experiments, but there was no response to carbon enrichment. Thus it was concluded that the phytoplankton were limited by both phosphorus and nitrogen.

Although these experiments suggest that nitrogen and phosphorus were deficient relative to carbon, Aphanizomenon is able to fix nitrogen (Stewart et. al. 1967, Stewart 1968, Granhall and Lundgren 1971), and concentrations of soluble phosphorus in the lake were high when growth rates were highest. Thus phosphorus and nitrogen may have been the limiting nutrients, but algal production probably was limited not by nutrients but by other factors, probably those affecting light attenuation, as described below.

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SECTION X

INTEGRAL PHOTOSYNTHESIS AND LAKE PRODUCTIVITY

Daily photosynthesis at the average depth where illumination is optimal (p_{max}) depends upon chlorophyll concentration (c) and maximum specific photosynthesis (P_{max}):

$$p_{max} \equiv cP_{max} \quad . \tag{1}$$

Daily integral photosynthesis (Σp) is the area enclosed by a depth-profile of photosynthesis. This area may be set equal to the area of a rectangle. If one side of the rectangle equals the rate of photosynthesis at the average depth where illumination is optimal (p_{max}), then

$$z_i \equiv \Sigma p / p_{max} \quad , \tag{2}$$

where z_i is the length of the other side (Talling 1957b). If the average intensity of photosynthetically-active radiation at the surface is I_o, and chlorophyll is uniformly distributed in the photic zone, then

$$I_{z_i} = I_o \, e^{-z_i (k_c c + k_w)} \quad , \tag{3}$$

where I_{z_i} is the average intensity at the depth z_i, k_c is the attenuation by chlorophyll, c is the chlorophyll concentration, and k_w is the attenuation by the water itself and by substances other than chlorophyll dissolved or suspended in it. Therefore,

$$z_i = \frac{\ln\left(\frac{I_o}{I_{z_i}}\right)}{k_c c + k_w} \quad , \tag{4}$$

The depth z_i increases to a maximum as chlorophyll concentrations decrease,

$$\lim_{c \to 0} z_i = \frac{\ln\left(\frac{I_o}{I_{z_i}}\right)}{k_w} \quad , \tag{5}$$

and it decreases as chlorophyll concentrations increase:

$$\lim_{c \to \infty} z_i = 0 \, . \tag{6}$$

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Thus

$$\Sigma p = \frac{\ln\left(\frac{I_o}{I_{z_i}}\right)}{k_c c + k_w} cP_{max} \quad , \tag{7}$$

$$= z_i c P_{max} \quad , \tag{8}$$

$$= z_i \, p_{max} \quad . \tag{9}$$

The product of z_i and c is the quantity (mg m^{-2}) of chlorophyll above the depth z_i. If this quantity is designated as c_i, then

$$\Sigma p = c_i P_{max} \quad . \tag{10}$$

Thus maximum photosynthesis (p_{max}) increases but the depth z_i decreases as chlorophyll concentrations (c) increase, provided that maximum specific photosynthesis (P_{max}) and the component optical terms of z_i are constant or less variable than chlorophyll concentrations. These constraints evidently pertain to Shagawa Lake as to Lake Minnetonka (Megard 1972), so that the ratio $\Sigma p/p_{max}$ ($=z_i$, equation 2) decreases systematically as chlorophyll concentrations increase. Consequently the depth z_i may be estimated from the chlorophyll concentration without measuring light intensities (Fig. 7-A). This makes it possible to estimate integral photosynthesis at any locality with equation (9) from chlorophyll concentration (c) and maximum photosynthesis (p_{max}), which are both easy to measure.

The instantaneous values of k_w and k_c are difficult to measure independently but their mean values may be evaluated from the regression of $\Sigma p/p_{max}$ on chlorophyll. The relationship between $\Sigma p/p_{max}$ ($=z_i$) and chlorophyll concentrations for the depth profiles of integral photosynthesis at Station A is shown in Fig. 7-A. Inspection of the datum points indicates that the value of z_i at zero chlorophyll (limit $c \to 0$ z_i) is approximately 3 m. Mean daily values of $\ln (I_o/I_{z_i})$ range between 2 and 3.5, but the most frequent value is 2.7 (Rhode et. al. 1958; Vollenweider 1965, 1969, 1970). If the latter value is chosen, then the mean value of k_w [$= \ln(I_o/I_{z_i})/\lim\, c \to 0\ z_i$] in Shagawa Lake is 0.9 m^{-1}. The curve in Fig. 7-A is that obtained by solving equation (4) at different chlorophyll concentrations (c) for the case where $\ln (I_o/I_{z_i})$ is 2.7, k_w is 0.9 m^{-1} and k_c is 0.03 m^2 (mg chlorophyll)$^{-1}$ (Table 11). These values of k_w and k_c are both higher than in Lake Minnetonka, where k_w and k_c derived in the sam way are 0.7 and 0.015 respectively (Megard 1972).

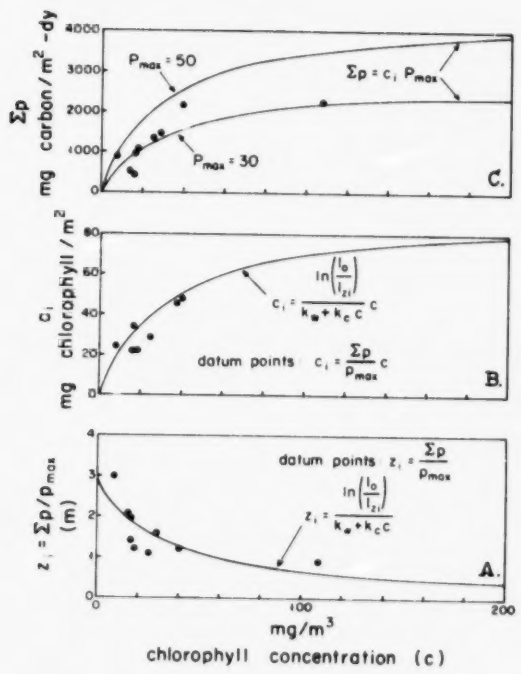


Figure 7. The relationships among chlorophyll concentrations (c) and the depth coefficient z_i (panel A); the quantity of chlorophyll above the depth z_i, c_i (Panel B); and integral photosynthesis, Σp (Panel C).

Table 11. Parameters for the photosynthetic system of the phytoplankton in Shagawa Lake if k_w is 0.90 m^{-1}, k_c is 0.03 m^2(mg chlorophyll)$^{-1}$, and $\ln(I_o/I_{z_i})$ is 2.7.

1	2	3	4	5	6	7
c	$k_c c$	$k_w + k_c c = \alpha$	$\frac{\ln(I_o/I_{z_i})}{\alpha} = z_i$	$c_i = z_i c$	$\Sigma p = c_i P_{max}$ $P_{max} = 30$	$P_{max} = 50$
0	0	0.9	3.0	0	0	0
5	.15	1.05	2.6	13	390	650
10	.30	1.2	2.2	22	660	1100
20	.60	1.5	1.8	36	1080	1800
30	.90	1.8	1.5	45	1350	2260
40	1.20	2.1	1.3	52	1560	2600
60	1.80	2.7	1.0	60	1800	3000
80	2.40	3.3	0.8	66	1980	3300
100	3.00	3.9	0.7	69	2060	3460
150	4.50	5.4	0.5	75	2240	3750
200	6.00	6.9	0.4	78	2360	3900
1000	30.00	30.9	0.09	90	2700	4500
units: mg chl. m^{-3}	m^{-1}	m^{-1}	m	mg chl. m^{-2}	mg carbon m^{-2} dy^{-1}	

If $\ln (I_o/I_{z_i})$ is relatively constant, then the limits of integral photosynthesis by a population with a particular density are imposed by the prevailing values of k_c, k_w, and P_{max}. The numerical values of z_i, c_i, and Σp for two values of P_{max} that correspond to the values of k_w and k_c estimated for Shagawa Lake are shown in Table 11, and the resulting curves are shown in Fig. 7. It is notable that the attenuation of photosynthetically-active radiation by chlorophyll ($k_c c$) exceeds attenuation by the water alone (k_w) where chlorophyll concentrations exceed 30 mg m^{-3} (Table 11, column 2). Where chlorophyll concentrations are 100 mg m^{-3}, the total attenuation coefficient, α (= $k_w + k_c c$), is 3.9 m^{-1}, z_i is only 0.7 m, and c_i is only 69 mg chlorophyll m^{-2}.

Large increments of chlorophyll above 50 mg m^{-3} produce small increments of c_i and Σp; a four-fold increase of chlorophyll, from 50 to 200 mg m^{-3} increases c_i and Σp only 50% (Fig. 7). Integral photosynthesis ranges between 2 and 4 g carbon m^{-2} dy^{-1} where chlorophyll concentrations exceed 100 mg m^{-3}, depending mostly upon variations of P_{max}; variations of population densities have little effect.

The highest integral photosynthesis measured at station A was 2.7 g carbon m^{-2} dy^{-1} on 31 August, when chlorophyll concentrations ranged from 977 mg m^{-3} at the surface to 220 mg m^{-3} at 1 m, but integral photosynthesis was almost that high (2.1 mg m^{-3}) on 17 August and 25 August, when chlorophyll ranged between 40 and 105 mg m^{-3} (Fig. 3).

The range of maximum specific photosynthesis in Shagawa Lake is about the same as in Lake Minnetonka (Megard 1972), but the upper limits for integral photosynthesis are lower in Shagawa because the attenuation coefficients for photosynthetically-active radiation are larger than in Lake Minnetonka. The high attenuation coefficients not only limit integral photosynthesis, they also prevent the population densities from becoming high enough to utilize all the dissolved phosphorus.

Equations 7-10 are strictly applicable only where phytoplankton is uniformly distributed in the photic zone. However, algal population densities at a particular locality in Shagawa Lake may change radically during a day, and the phytoplankton are stratified in the photic zone during August. Thus even measurements of photosynthesis at depth intervals <u>in situ</u> cannot provide reliable estimates of integral photosynthesis at a particular time or place, because both algal abundance

and the optical properties of the water may vary substantially during the period of measurement. However, the effects of these ephemeral variations will tend to cancel during long time intervals, so that the mean daily value of integral photosynthesis for the lake as a whole may be estimated from the mean chlorophyll concentrations (c) and mean specific photosynthesis (P_{max}) with equation (8).

The area under curves for chlorophyll and specific rates of photosynthesis vs. time in Fig. 4 were determined with a planimeter, and the weighted mean value of c for the period from June through October was found to be 34 mg chlorophyll m^{-3} and that of P_{max} to be 29 mg carbon (mg chlorophyll)$^{-1}$ dy^{-1}. The mean value of z_i may be estimated from the regression of $\Sigma p/P_{max}$ on chlorophyll (Fig. 7-A), which indicates that the value of z_i where chlorophyll is 34 mg m^{-3} is about 1.5 m. Thus, by substitution in equation (8), the weighted mean value of integral photosynthesis for the entire lake is 1.5 g carbon m^{-2} dy^{-1} or about 220 g carbon m^{-2} for the 150-day period. The ice usually melts in mid-April and the lake usually freezes in late November. Integral gross photosynthesis is probably about 0.5 g carbon m^{-2} dy^{-1} during spring and November. If the total open water season is 75 days longer than the study period, then the additional gross photosynthesis is about 40 g carbon m^{-2}, and the total gross photosynthesis for the open-water season is approximately 250-300 g carbon m^{-2}.

The daily influx of organic material from the sewage effluent is very much smaller than the daily production of organic carbon by the phytoplankton in the lake. If average daily integral photosynthesis is 1.5 g carbon m^{-2}, then the average total production for the entire lake (9.6×10^6 m^2) is 14,000 kg carbon dy^{-1}. The rated capacity of the treatment plant is 4×10^6 liters per day. If the effluent contains 55 mg liter^{-1} organic material, as is typical for a secondary sewage effluent (Amer. Chem. Soc. 1969), and if the organic material is 50% carbon, then the influx from the treatment plant is about 100 kg carbon dy^{-1}. Thus, although the treatment plant contributes about 70% of the phosphorus that enters the lake, it contributes less than 1% of the organic carbon.

The Burntside River at the west end of the lake contributes most of the water, but the sewage outfall at the south side contributes most of the phosphorus. The basin also has an irregular shape with many islands that might

partition the water into discrete masses with somewhat different nutrient concentrations and productivities. However, the mean chlorophyll concentrations, specific rates of photosynthesis, and total phosphorus concentrations at the sampling stations are not significantly different from each other, and there are no gradients with respect to the major sources of water or nutrients (Table 12). The highest average phosphorus concentration is at Station B, near the lake's outlet, not at Station A, where the sewage effluents enter. On the other hand the lowest average phosphorus concentration is at Station C, in mid-lake, not at the station near the entrance of the Burntside River. Although a more intensive sampling program might reveal consistent differences between the stations, it appears that the water and dissolved substances entering the lake are distributed uniformly throughout the basin by currents and that the lake is a well-mixed system despite the contrasting water quality of the inflowing streams and irregularities of the basin itself.

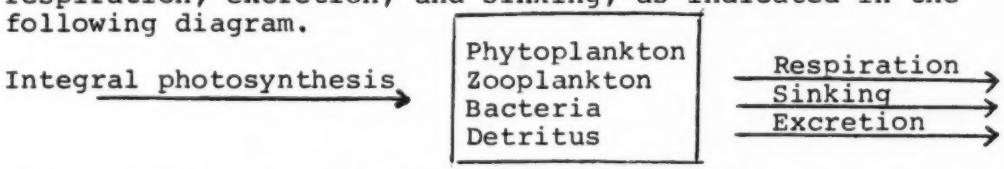
Table 12. Means and standard deviations for chlorophyll concentrations (c), maximum specific photosynthesis (P_{max}) and total phosphorus concentrations (F_t) in Shagawa Lake, June through October, 1970.

	c	P_{max}	F_t
Station A	31 ± 30	34 ± 12	78 ± 42
B	27 ± 15	24 ± 10	83 ± 55
C	36 ± 28	29 ± 9	74 ± 39
D	30 ± 22	33 ± 11	75 ± 43
E	37 ± 35	30 ± 11	78 ± 47
F	28 ± 18	31 ± 14	76 ± 50

SECTION XI

POPULATION REGULATION

Algae, bacteria, zooplankton, and organic detritus are all composed of particulate organic carbon. Particulate organic carbon produced by algae in the photosynthetic zone is distributed throughout the epilimnion by turbulent mixing. The particulate organic carbon may be incorporated into zooplankton, bacteria, and detritus after it is produced by algae. It may be degraded to soluble carbon compounds by respiration and excretion, or it may be lost by sinking. Thus the particulate organic carbon in the mixed layer beneath a unit of lake surface is a functional unit, with gains due to photosynthesis and losses due to respiration, excretion, and sinking, as indicated in the following diagram.



The organic carbon contributed to Shagawa Lake by sewage is much smaller than that produced by the phytoplankton, and the quantity contributed by other sources in the watershed is probably negligible also. It should be emphasized that predation by zooplankton is not a loss of particulate organic carbon from the mixed layer; it is only a transfer between groups of organisms.

Strickland (1960) has indicated that it is neceasary to measure both the density of a population and its rate of production in order to assess the fertility of a water mass. If both population densities and rates of production are measured in units of particulate organic carbon, then the specific rate of change, specific rate of production, and specific rate of loss may be calculated.

Although concentrations of particulate organic carbon were not measured in Shagawa Lake, they may be estimated from the relationship between the concentrations of chlorophyll and particulate material in the water (Fig. 8). The slopes of the equations for the regression of chlorophyll on particulate material indicate that chlorophyll concentrations during August are about 2% as large as the concentrations of particulate material. Hence the ratio of particulate material to chlorophyll is about 50:1.

The particulate material probably contains about 10% inorganic material and 40% carbon (Strickland 1965, Table

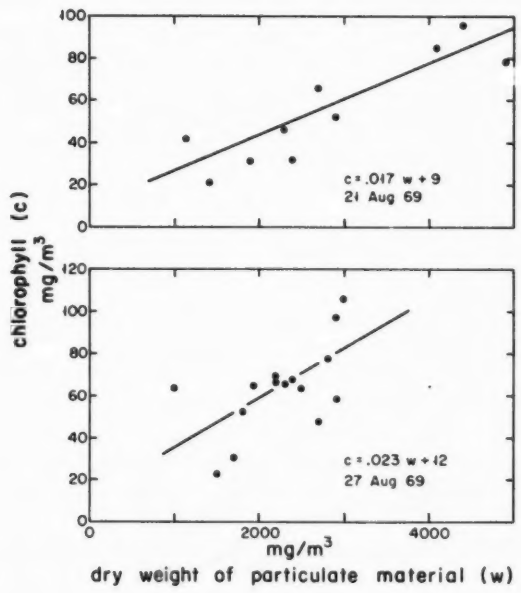


Figure 8. Regression of chlorophyll concentrations on the dry weight of particulate material in water from the mixed layer during August, 1969. Data provided by the staff of the Shagawa Eutrophication Project.

3). Therefore the ratio of particulate organic carbon to chlorophyll (f) in Shagawa Lake is probably about 20:1. The ratio for marine diatoms was 60 in nutrient-poor water and 25 in coastal water that contained excess nitrogen and phosphorus (Strickland 1965, Table 6). The ratio in Lake 227 in the Experimental Lakes Area of northwest Ontario was 300 before the lake was artificially fertilized, but it decreased after fertilization to 115 in 1969 and to 55 in 1970. Small flagellated algae dominated the phytoplankton before it was fertilized, but blue-green algae dominated afterward (Schindler 1971). The changing ratio in this lake suggests that blue-green algae contain more chlorophyll than others, or that the proportion of the particulate material that contains chlorophyll increases in enriched lakes, or both. The ratio apparently decreases as nutrients increase in both the sea and lakes; perhaps continued fertilization of Lake 227 would decrease the ratio to the value in Shagawa.

The existing quantity of particulate organic carbon in the mixed layer beneath a unit of lake surface (w') is

$$w' = cz_m f \quad , \tag{11}$$

where c is the chlorophyll concentration, z_m is the thickness of the mixed layer, and f is the ratio of carbon to chlorophyll.

If the quantity of particulate organic carbon changes at a constant rate during an interval between sampling dates, then the specific rate of change (r) during an interval may be computed from the quantity present at the beginning (w'_o) and end (w'_t) of the interval with the equation

$$r = \frac{1}{0.5\ (w'_o + w'_t)} \quad \frac{w'_t - w'_o}{t} \quad , \tag{12}$$

where t is the duration (days) of the interval.

The specific rate of change depends upon the specific rate of production (μ) by photosynthesis and the specific rate of loss (λ) by respiration, excretion and sinking:

$$r = \mu - \lambda$$

Specific rates of production may be estimated directly from measurements of integral gross photosynthesis with the oxygen method. Various studies have shown (cf. Eppley 1968) that measurements of photosynthesis with the ^{14}C technique are in fact measurements of the net

increase of particulate organic carbon. The oxygen method should then yield estimates of gross production because it includes a correction for losses by respiration. As with the ^{14}C method, losses by sinking are prevented because the plankton is enclosed in bottles. There is no correction for losses by excretion, but this error is probably small and offset by increases of population densities during the time that photosynthesis is measured.

If the average daily rate of production during a time interval is an average of the rates at the beginning (p_o) and the end (p_t) of the interval and if the specific rate of change is constant, then the specific rate of production may be estimated with the equation

$$\mu = \frac{0.5\ (p_o + p_t)}{0.5\ (w'_o + w'_t)} \quad . \qquad (14)$$

The specific rate of loss may be computed by substituting the estimates of r and μ in equation (13).

The estimated specific rates of change, of production, and of loss for particulate organic carbon in the mixed layer are shown in Table 13. It was assumed that the thickness of the mixed layer (z_m) was constant at 5 m and that the ratio of carbon to chlorophyll (f) observed in August (20) also prevailed in June and July.

The quantity of particulate organic carbon increased approximately 5-fold during August, but average daily production increased only about 50%. The specific rate of change was approximately 0.02 dy^{-1} during July, it ranged between 0.04 and 0.07 during August, and it decreased to -0.22 during the rapid decrease in early September. Specific rates of production and of loss were high, 0.49 and 0.47 respectively in late July, before population densities began to increase most rapidly. The specific rate of production decreased from 0.50 to 0.16 during the rapid increase of population densities in August, but the specific rate of loss decreased more rapidly, from 0.48 to 0.08. The rapid decrease of population densities in early September occurred when the specific rate of loss increased to 0.37 without a concurrent increase of specific production.

These calculations suggest that population densities increased rapidly during August because specific rates of loss decreased faster than specific rates of production. Furthermore the rapid decrease in early September was produced by an increase in the loss rate. Thus the buoyancy implied by the stratification of chlorophyll

Table 13. Specific rates of change (r), of production (μ), and of loss (λ) for the particulate organic carbon in the mixed layer of Shagawa Lake.

Interval	ave. part. org. carb. in mixed layer $0.5\ (w'_o + w'_t)$	ave. production of part. org. carbon $0.5\ (p_o + p_t)$	r	μ	λ
3 Jun-17 Jun	1600	535	+.045	0.33	0.28
17 Jun-2 Jul	1800	595	-.022	0.33	0.34
2 Jul-22 Jul	1800	880	+.017	0.49	0.47
22 Jul-6 Aug	2450	1230	+.020	0.50	0.48
6 Aug-17 Aug	4750	1470	+.073	0.30	0.23
17 Aug-25 Aug	7900	1770	+.038	0.22	0.18
25 Aug-31 Aug	11850	1900	+.075	0.16	0.08
31 Aug-5 Sep	9150	1390	-.220	0.15	0.37

during August (Fig. 3) appears to be a critical mechanism of population regulation by Aphanizomenon; greater buoyancy apparently reduced losses by sinking and permitted population densities to increase rapidly even though maximum specific photosynthesis decreased. Moreover, the rapid decrease in September probably occurred because Aphanizomenon lost its ability to regulate its buoyancy.

In contrast to many other algae Aphanizomenon is neutrally buoyant (Smayda 1969). The buoyancy of blue-green algae depends upon the presence of gas vacuoles (Walsby 1972, Fogg and walsby 1971). Oscillatoria redeckii produces vacuoles at low light intensities (Whitton and Peat 1969). The vacuoles of Anabaena flos-aquae collapse at high light intensities if CO_2 is present (Walsby 1969). The vacuoles are located near photosynthetic membranes (Smith and Peat 1967), and the collapse may be due to the turgor pressure of the cells, which increases as sugars are produced during photosynthesis. Therefore, blue-green algae tend to produce gas vacuoles when they are in the aphotic zone of the epilimnion and to lose them in the photic zone. The production and collapse of vacuoles may be fast enough to result in diurnal movements (Fogg 1969, Fogg and Walsby 1971) such as those implied by the distribution of Anabaena in a Nile reservoir (Talling 1957c), where the algae tend to be uniformly distributed early in the morning and concentrated near the surface in late afternoon.

In Shagawa Lake, high levels of extractable phosphorus in early August may have enhanced the ability of Aphanizomenon to produce vacuoles, which reduced sinking rates and permitted the population to become stratified. The low levels of extractable phosphorus in early September may have inhibited photosynthesis and vacuole regulation, thereby increasing sinking rates, and contributing to the rapid decrease of population densities.

Even though several very high population densities were excluded from the calculation of average population densities during August and September, the quantity of particulate organic carbon in the mixed layer beneath 1 m^2 of lake surface may have been overestimated because the phytoplankton were stratified. If population densities were overestimated, then the estimates of r and λ are too high and those of μ are too low.

SECTION XII

STEADY STATES FOR POPULATION DENSITIES AND INTEGRAL PHOTOSYNTHESIS

The relationships between the quantity of particulate organic carbon in the mixed layer, production, and loss may be expressed as

$$w'_o + \Sigma p - \lambda w' = w'_x \quad , \tag{15}$$

where λ is the fraction of the particulate organic carbon that is lost each day by respiration, excretion, and sinking.

If the quantity of particulate organic carbon does not change, then $w'_o = w'_x$ and $\Sigma p = \lambda w'$. Therefore,

$$\frac{\ln\left(\frac{I_o}{I_{z_i}}\right)}{k_w + k_c c} cP_{max} = \lambda(cz_m f) \quad . \tag{16}$$

Thus steady state population densities are defined by the intersection of curves for the production (Σp) and loss ($\lambda w'$) of particulate organic carbon in the mixed layer.

In Fig. 9, the quantity of particulate organic carbon beneath 1 m^2 of surface (w') is computed for a mixed layer (z_m) 5 m thick where the carbon:chlorophyll ratio (f) is 20. Integral photosynthesis is calculated for two cases, one where P_{max} is 50 and the other where P_{max} is 30 mg carbon (mg chlorophyll)$^{-1}$ dy^{-1}. In both cases k_w is constant at 0.9 m^{-1} and k_w at 0.03 m^2 (mg chlorophyll)$^{-1}$ If P_{max} is 30 mg carbon (mg chlorophyll)$^{-1}$ dy^{-1} and the loss (λ) is 0.5 dy^{-1} (Fig. 9-A), then the maximum specific rate of change ($r_{1\ max}$) occurs where chlorophyll concentrations (c) are 10 mg m^{-3} and the quantity of particulate organic carbon in the mixed layer (w') is 1000 mg m^{-2}. However, integral photosynthesis and losses are both 50% of the quantity of particulate organic carbon in the mixed layer when chlorophyll concentrations reach 25 mg m^{-3}. Losses exceed production at higher chlorophyll concentrations, so plankton populations with these specified parameters will become stationary at 25 mg chlorophyll m^{-3}. If the rate of loss decreases to 0.25 dy^{-1} then the maximum rate of change ($r_{2\ max}$) occurs when chlorophyll concentrations reach 30 mg m^{-3}, and the stationary chlorophyll concentration is 80 mg m^{-3}.

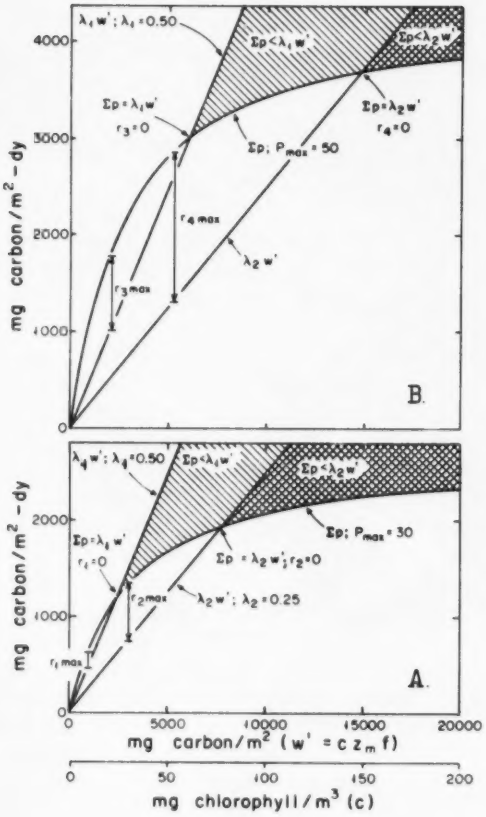


Figure 9. Steady state population densities defined by two values of maximum specific photosynthesis (P_{max}) and loss rates.

If, on the other hand, P_{max} increases to 50 (Fig. 9-B), then the maximum rates of increase ($r_{3\ max}$ and $r_{4\ max}$) and the stationary chlorophyll concentrations are correspondingly higher. The stationary chlorophyll concentrations are 60 mg m^{-3} where the loss is 0.50 dy^{-1} and 150 mg m^{-3} where the loss is 0.25 dy^{-1}.

Thus it appears that the chlorophyll concentrations during July (about 20 mg m^{-3}) represent nearly steady state population densities for the prevailing optical conditions when maximum specific photosynthesis is approximately 30 mg carbon (mg chlorophyll)$^{-1}$ dy^{-1} and loss rates are approximately 0.5 dy^{-1}.

SECTION XIII

DISCUSSION

The calculations described above indicate the degree to which population densities may be influenced by changes in loss rates without changing other components of the system. It is frequently assumed that rapid increases of population densities are caused by high rates of specific photosynthesis induced by high concentrations of limiting nutrients. However, specific rates of photosynthesis decreased during rapid growth in Shagawa Lake even though concentrations of dissolved phosphorus were high. It appears that the high attenuation coefficient for photosynthetically-active radiation together with high loss rates prevented the phytoplankton from utilizing dissolved phosphorus as rapidly as it was delivered, and that population densities increased during August because loss rates decreased more than production rates. In this case rates of loss appear to be regulated by changes in the buoyancy of the dominant alga. Circumstantial evidence suggests that the buoyancy of Aphanizomenon does not depend only upon nutrient concentrations in the ambient water but also upon intricate relationships among the optical conditions, rates of chlorophyll synthesis, and rates of phosphorus uptake.

The data from Shagawa Lake suggest that both production rates and loss rates are influenced by algal nutrition. The relationship between loss rates and nutrients cannot be defined because there are at least three different kinds of losses. However, the primary production of particulate organic carbon can only be accomplished by photosynthesis. Photosynthesis and nutrient uptake are separate processes, but if photosynthesis is a function of nutrient uptake, then the maximum specific rate may be expressed in terms of Michaelis-Menton kinetics (Dugdale 1967, Thomas 1970):

$$P_{max} = \hat{P}_{max} \frac{S}{k_s + S} \quad , \qquad (17)$$

where $\hat{P}_{max}$ is maximum specific photosynthesis where the concentration of the limiting nutrient (S) is saturating and k_s is the nutrient concentration where $P_{max} = \hat{P}_{max}/2$. Thus, integral photosynthesis may be written

$$\Sigma p = \frac{\ln\left(\frac{I_o}{I_{z_i}}\right)}{k_w + k_c c} \; c \, \hat{P}_{max} \; \frac{S}{k_s + S} \quad . (18)$$

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Experiments by Thomas (1970) on natural populations of marine phytoplankton indicate that it will be difficult to evaluate $\hat{P}_{max}$ and k_s for natural assemblages, but the role of nutrients cannot be defined precisely unless this is done. Fortunately P_{max} may be evaluated easily without measuring $\hat{P}_{max}$ or k_s, although the highest values of P_{max} measured in Shagawa, 50-60 mg carbon (mg chlorophyll)$^{-1}$ dy^{-1} may approximate $\hat{P}_{max}$ for Aphanizomenon in this lake.

The general relationship among variations of population densities, maximum specific photosynthesis, and loss rates are shown in Fig. 10. If nutrient enrichment increases P_{max} without changing losses then integral photosynthesis increases from Σp_1 to Σp_2 and the quantity of particulate organic carbon in the mixed layer increases from w_1' to w_2'. However if nutrient enrichment increases P_{max} and simultaneously reduces λ, then Σp_3 and w_3' are higher than Σp_2 and w_2'.

The intersection of the curves define steady states for Σp and w', but no steady state exists is losses exceed integral photosynthesis at all population densities (Fig. 10-D).

An algal species may become more abundant than others in its environment if its mechanisms of nutrient uptake and photosynthesis are more efficient, if it has smaller losses, or both. Aphanizomenon belongs to an ancient group of blue-green algae that occurs in the oldest fossiliferous rocks (Barghoorn and Tyler 1965, Whittaker 1969). Its mechanisms of nutrient uptake and photosynthesis may be less efficient than those of other algae that have developed specialized organelles during their evolution. Consequently, the ability to regulate buoyancy conferred by its gas vacuoles may be not only an important mechanism that enables Aphanizomenon to produce dense blooms in eutrophic lakes but also the mechanism that has enabled it to compete with less conservative algae since Precambrian times.

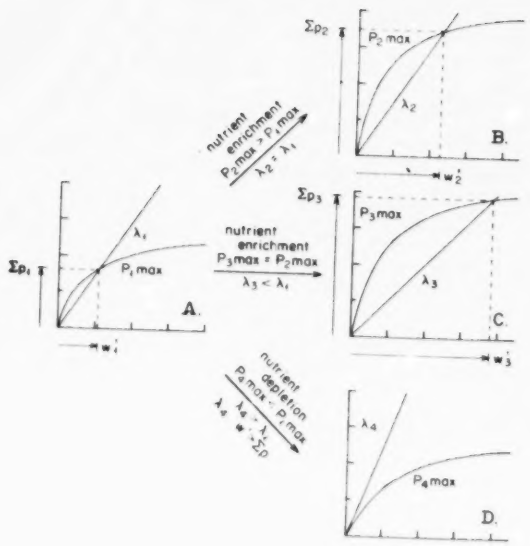

Figure 10. The general relationships among the quantity of particulate organic carbon in the mixed layer (w'), integral photosynthesis (Σp), maximum specific photosynthesis, and loss rates.

SECTION XIV

LIST OF SYMBOLS

c	Concentration of chlorophyll *a*
p_{max}	Maximum daily photosynthesis per unit volume of water at the average depth of optimal illumination
P_{max}	Maximum daily photosynthesis per mg chlorophyll at the average depth of optimal illumination
Σp	Daily integral photosynthesis
z_i	The depth given by the ratio $\Sigma p : p_{max}$
I_o	The daily average intensity of photosynthetically-active radiation at the lake surface
I_{z_i}	The daily average intensity of photosynthetically-active radiation at the depth z_i
e	The base of natural logarithms
k_c	Attenuation of photosynthetically-active radiation by a unit chlorophyll concentration
k_w	Attenuation of photosynthetically-active radiation by the water and by substances other than chlorophyll dissolved and suspended in the water
α	The total attenuation coefficient for photosynthetically-active radiation
c_i	The quantity of chlorophyll above the depth z_i
w	The concentration of particulate material in the water
w'	The quantity of particulate organic carbon in the mixed layer beneath a unit surface area
z_m	The thickness of the mixed layer (epilimnion)
f	The ratio of the concentration of particulate organic carbon to the concentration of chlorophyll in the water
r	The specific rate of change for particulate organic carbon in the mixed layer

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μ The specific rate of production of particulate organic carbon in the mixed layer

λ The specific rate of loss of the particulate organic matter in the mixed layer by respiration, excretion, and sinking

SECTION XV

ACKNOWLEDGEMENTS

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